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Cyclic abundance fluctuations in a completely isolated population of *Euphydryas maturna*

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Abstract. A highly isolated and the last autochthonous Czech Republic population of the endangered *Euphydryas maturna* (Lepidoptera: Nymphalidae) is monitored since 2001 by larval nests counts. The 20 years` time series displays remarkable abundance fluctuations with peak-to-peak period 11 years, peak numbers >150 and bust numbers <15 larval nests (arithmetic and harmonic means: 92.6 and 36.3). Establishment of more favourable management of the site probably heightened and prolonged the boom phase but did not alter the overall pattern. We attribute the cycling to pressures of natural enemies. Climatically unfavourable years appear deepening the bust phase. Species displaying such fluctuations cannot be conserved within a single site, which is being addressed by ex-situ breeding of the Czech stock and recent reestablishment of two additional populations, with the aim to achieve asynchronous dynamics of the local populations and eventually stabilise the regional metapopulation.

Introduction

Interannual abundance fluctuations are familiar phenomenon in Lepidoptera (Myers 1988; Peltonen et al. 2002; Bungten et al. 2009), including the much studied Melitaeinae checkerspot butterflies (Nymphalidae) (Ford and Ford 1930; McLaughlin et al. 2002; Ehrlich and Hanski 2004; Gros 2012). Irregular fluctuations are attributable to abiotic factors, e.g. weather (Stange et al. 2011; Csóka et al. 2018). More regular abundance changes may be caused by regularly occurring disturbances, such as felling and regrowth at woodland clearings, to which sun-demanding species react by vacating and recolonising suitable sites (Warren 1987). Finally, regular fluctuations independent on the sites` dynamics may result from pressures of natural enemies, such as predators, parasitoids or diseases, lagging after the dynamics of their hosts (Berryman 1996; Dwyer et al. 2004).

Detecting the latter phenomena requires long-term monitoring data (Johns et al. 2016) and may be obscured by migrations of individuals among local populations, which may display mutually independent local dynamics (Myers 2000). Here, we report a case of cyclic abundance changes in a population of an endangered woodland checkerspot butterfly, to which immigration has been practically impossible due to its complete isolation.

Euphydryas maturna (Linnaeus, 1758) is an Eurosiberian species, distributed from eastern France across Central Europe and southern Scandinavia to Urals and eastwardly to Baikal region (cf. Rakosy et al. 2012). It is threatened in all occupied European countries due to association with open-canopy broadleaf woodlands with species-rich herb layer, which considerably declined across the continent with the cessation of such historical uses as forest pasture or coppicing (Konvička et al. 2005; Freese et al. 2006; Fischer et al. 2017; Mayer 2020). The butterfly is protected under EU Habitat Directives, and increasing number of states pursue active conservation measures, including government-funded restoration of historical forestry practices (Dolek et al. 2018). Its decline was particularly severe in the Czech Republic, where it was historically recorded from 29 (out of 675) grid mapping squares but currently survives at a single locality. The past distribution included open canopy structures in floodplain forests along major rivers and sparse oak-hornbeam woodlands in colline altitudinal belt (Benes and Konvicka 2002). The severity of the decline is attributable to complete abandonment of coppicing management in the country during 20th century and ensuing darkening of the woodlands (cf. Chytry 2012). The species was even considered nationally extinct by late 20th century (Vrabec 1994), when Vrabec (1998, 2001) discovered a hitherto unknown population, situated ≈12 km from a historically known and then already unoccupied locality. In this population, a mark-recapture study in 2002 estimated alarmingly low adult numbers, ≈200 (Konvička et al. 2005). Since then, the population has been monitored annually by larval nests counts. Particularly low counts in 2008 and 2009 (Čížek and Konvička 2009) prompted issuing a Species Action Plan [SAP], which strives to the improve habitat conditions by transferring the current habitat, high forest with transient clearings, towards more open canopy structure (AOPK ČR 2011). Vrabec et al. (2018, 2019) attributed the subsequent population increase to these management measures. The SAP also provided for establishing two ex-situ populations, based on stock from the last locality and intended for eventual reintroductions, or reinforcements.

By early 2021, the larval nests time series covers 20 seasons (2001–2020), which is enough for elucidating the temporal population dynamics.

Methods

The studied population inhabits a single woodland reserve, Dománovický les [= Dománovice forest], Central Bohemia (50.11N, 15.34E, altitude: 247 m, area 75 ha), situated amidst intensive farmland of Elbe river alluvium. It was established in 1989 to protect floristically rich oak-hornbeam forest on base-rich soils. Following the discovery of *E. maturna* population (Vrabec 1998), the reserve, expanded to 355 ha (it exceeds *E. maturna* distribution area) and became a site of European community interest, targeting conservation of this species (AOPK ČR 2011).

The life history of *E. maturna* in Central Europe (e.g., Gros 2002; Straka 2014; Fischer et al. 2017; Mayer et al. 2020), including the Czech site (AOPK ČR 2011), is known in much detail. The species is univoltine (late May – June), females oviposit batches of several hundred eggs at fresh *Fraxinus excelsior* leaves; rarely used alternative host plants are *Ligustrum vulgare* and

Viburnum opulus (Dolek et al. 2013). Larval feeding begins in communal silken nests. Larvae from these primary nests sometimes merge with others to form secondary nests (Vrabec 2001), and in the 3rd instar (late July – August), they disperse solitarily and enter quiescence and hibernation. In March – April, following the overwintering, they finish feeding first on forest floor herbs (with regionally differing preferences: Rakosy et al. 2012) and then at budding *F. excelsior*. Elsewhere in its wide distribution range, the ecology may considerably differ. For instance, mainly herbs are consumed by larvae in Finland (Wahlberg 2001), whereas *Fraxinus angustifolia* subsp. *pannonica* is used for pre-hibernation larval feeding in Pannonian basin (Rakosy et al. 2012).

The annual monitoring targets the primary larval nests, present from mid-July to mid-August depending on the season. Experienced persons equipped with binoculars systematically survey the site, using the knowledge of the nests` distribution in previous years. They systematically survey forest clearings, open canopy patches, track verges and edges, checking *F. excelsior* saplings and low-hanging (<12 m) branches of taller trees. The alternative host plants are also surveyed. For each nest detected, GPS coordinates are recorded. Each year, the map of the spatial distribution of nests is created to advice woodland managers. It takes 6–10 person-days to survey the entire locality.

In four seasons (2002, 2016, 2017, 2019), adult numbers were estimated by mark-recapture procedures (details: Vrabec et al. 2019). We relate here the adult number estimates to larval nests numbers in the same season.

Results

During the 20 monitoring seasons, two population peaks occurred, both followed by busts (Figure 1). In the peak years, the population reached 164 (2006) and 202 (2017) larval nests. The peaks were preceded by three (2003–2005) or five (2013–2016) seasons with nest numbers >100. Each peak was followed by a season with diminished but still quite high numbers (2007, 2018), and then by a bust, with the nest numbers merely ≈8% of the peaks. The lowest nest numbers observed were

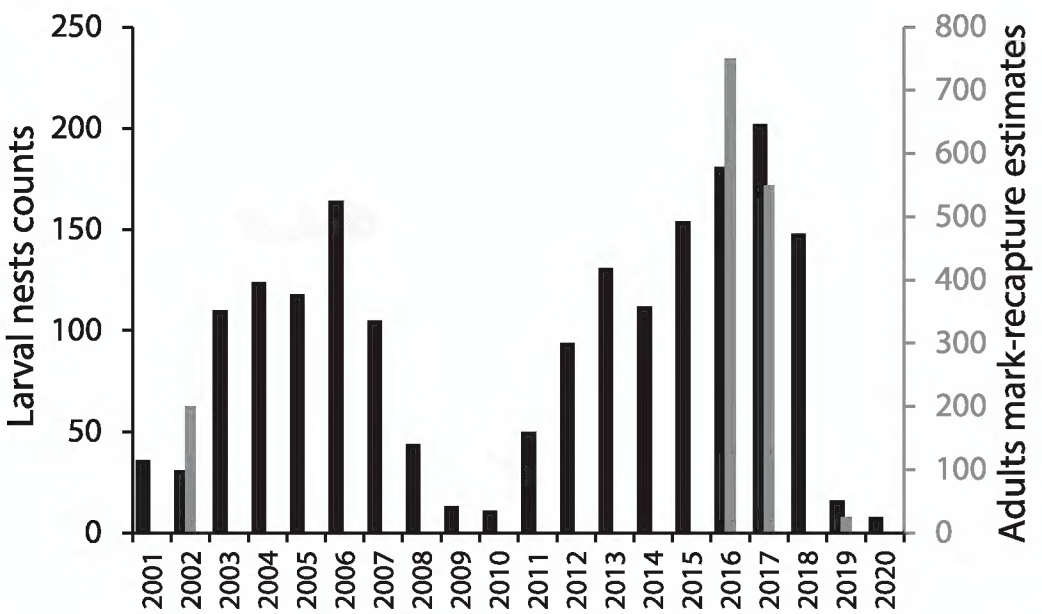

Figure 1. Abundances of *Euphydryas maturna* larval nests in its last Czech Republic population, as detected by annual monitoring surveys, and adult numbers estimates based on mark-recapture surveys. The adult estimates are from Konvička et al. (2005) – 2002, Vrabec et al. (2019) – 2016, 2017, and unpublished data by AOPK ČR 2019.

11 (2010) and 7 (2020). This resulted into a great discrepancy between arithmetic (=92.6 ± 61.92SD) and harmonic (=36.3) means of yearly numbers. Whereas the length of the first cycle cannot be ascertained from the existing data, the peak-to-peak length of the second cycle was 11 years.

Semiquantitative observations of adults and larval nests exist also for the years 1996–1998, following the discovery of the population. Then, the population appeared abundant (Vrabec and Jindra 1998), contrasting with the low numbers in the 2001–2002. Due to a smaller area then examined, the 1996–1998 data cannot be used for direct comparison. Still, they indicate that the monitoring in 2001 started while the population was recovering from a preceding bust.

Based on the four year with mark-recapture data available, the adults : nests ratio is 3.7 (±2.10 SD), implying that ≈4 adults are necessary to produce one larval nests. The lowest ratio, 1.6, was found in the bust year 2019, and highest, 6.5, in the bust year 2002, so the ratios probably had little in common with the stage of the population cycle.

Notably, the development of nests numbers followed identical trajectory of increase, boom and bust prior to 2011, when the site was not actively managed for the species, and after 2011, under active management. Favourable management might had contributed to the longer plateau of nests number >100 during the second cycle and to the higher amplitude of the second peak. On the other hand, the second cycle displayed a steeper decline (90% reduction from 2018 to 2019).

Discussion

An isolated population of *Euphydryas maturna* in the Czech Republic undergoes cyclic abundance changes with ten-fold abundance difference between booms and busts and 11- years period. Such fluctuations were observed by previous authors, e.g., in Salzburg, Austria (Gros 2012), Steigerwald, Germany (M. Dolek, personal communication of unpublished data) and Hungary (Pecsenye et al. 2017a, b). Whereas the Austrian data reveal amplitude and period of the fluctuations very similar to the population monitored by us, the fluctuations in Steigerwald display less regular pattern of peaks and busts, but similar magnitude of declines during the busts, ≈10% of peak numbers. Such remarkable abundance changes are seriously diminishing the effective population size (Vucetich and Waite 1999), augmenting genetic threats to this endangered species (Pecsenye et al. 2017a). They also explain the elusive character of past distribution in the Czech Republic and elsewhere, with the species being repeatedly "lost" and "rediscovered" by recorders (cf. Vrabec 1994, 1998). The period of the fluctuations reported here is rather long, but fells withing the range known for cyclically fluctuating woodland moths, which spans from 3–8 years, e.g., in *Lymantria dispar* (Linnaeus, 1758), to 12–20 years, e.g., in *Choristoneura freemani* Razovski, 2008 (Myers 1988; Hlasny et al. 2016; Johns et al. 2016).

Although we can only speculate on drivers of the pattern, arm-race with natural enemies, frequently mentioned for woodland defoliating insects' abundance cycles (Berryman 1996; Dwyer et al. 2004), is the obvious suspect. The communal *E. maturna* eggs and larvae attract large numbers of predators (Vrabec and Jindra 1998) and parasitosis (Dolek et al. 2006; Straka 2014; Fischer et al. 2017; Mayer 2020); microbial or fungal infections are also possible. Until recently, rarity and legal protection of the species precluded quantifying infestation levels by experimental rearing of parasitoids, or DNA screening of entire larval nests. An indirect support for role of natural enemies is provided by spatial patterns of the larval nests distribution in peak and bust years (Figure 2). During the peaks, the nests tend to be distributed evenly across the inhabited forest, with concentration at appropriate open-canopy patches, whereas during bust phase, majority of the nests were

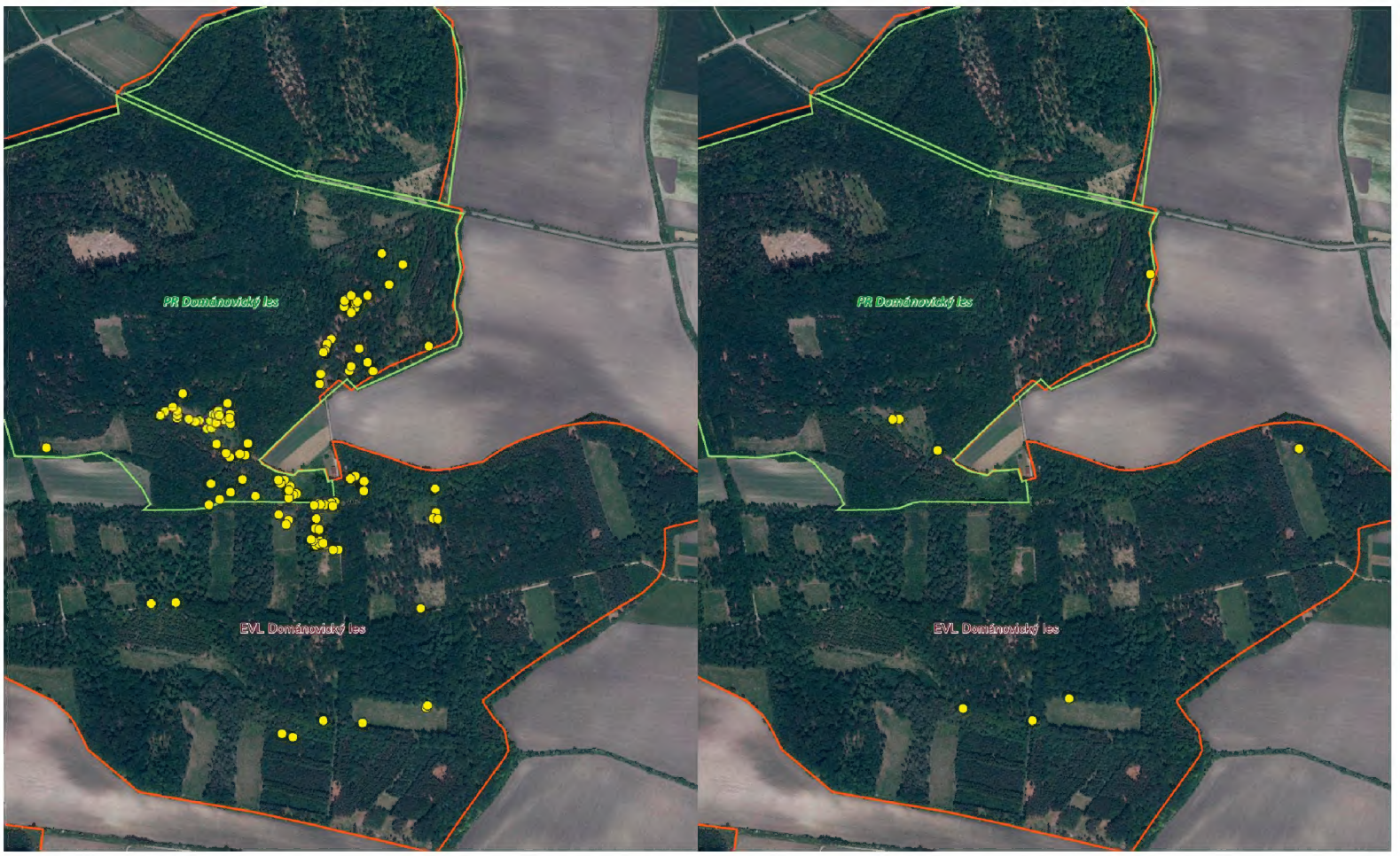

Figure 2. Examples of the GPS-recorded positions of *Euphydryas maturna* larval nests (yellow dots), showed for 2018, year with still rather high nests numbers, and 2020, year with the lowest count ever. Thin green line is the border of Dománovický les nature reserve [= PR], green, thin red line is the border of the Domáovický les Site of community interest [= EVL]. The nests are visibly concentrated in the centre of the occupied area in 2018, while proportionally more nests occur in peripheral positions in 2020.

found in marginal positions. Threats acting as contagions, including natural enemies or diseases, affect populations from centroids of their distributions towards peripheries, while the peripheries are more likely spared (Channel and Lomolino 2020). A complementary explanation for this spatial pattern may follow from biology of the natural enemies, for which it may be more difficult to locate peripherally situated hosts. For the butterfly, a trade-off may exist between development in a half-shaded mature forest, likely suboptimal microclimatically (Freese et al. 2006) but less exposed to natural enemies, and development at microclimatically suitable but infestation-exposed clearings (cf. Rothman and Roland 1998). Finally, a cyclical variation of the host plant chemical defences, complementary with fluctuations of parasitoids and known to affect, e.g., defoliating geometrid moths (Ossipov et al. 2014), may warrant investigation.

Despite the harmonic shape of the fluctuations (Figure 1), the dramatic population drop 2018/19 deserves attention. Besides of the cyclical pressures discussed above, unfavourable weather could have played a role. In the ex situ breeding, a third of larvae (≈70 out of ≈200; more precise counts would intolerably disturb the individuals) produced by 2018 spring adults (eclosed unusually early, during first half of May) pupated and produced 25 adults in September 2018. *Euphydryas maturna* thus produced a partial second (captive) generation. The rearing conditions were similar to the natural locality (a garden 18 km aerial distance apart, identical altitude, open-walled roofed structure). The year 2018 was exceptionally warm, historically the hottest ever. In natural conditions, such late-season adults would perish due to scarcity of nectar, honeydew and larval diet in advancing

autumn. Regretfully, we did not check for late-season adults in situ. Too fast development above some thermal thresholds and ensuing risk of lost autumn generations (Van Dyck et al. 2015) may even determine the geographic range of *E. maturna*, which copies the nemoral woodlands but does not reach to warmer regions of southern Europe. The mild 2018 winter was followed by Arctic spell in May 2019, which killed a half of the pupae during a dozen of nights with -0 °C temperatures, suggesting a lack of pupal cold hardiness in this species.

Regardless the causes, the fluctuating pattern resolves the contradictions in previous reports, which were based on shorter time frames. Warnings based on the low counts in 2002 (Konvicka et al. 2005) and again in 2009 (Cizek and Konvicka 2009) appeared as unnecessarily alarmist shortly thereafter (Krása and Pavlíčko 2014; Vrabec et al. 2018). However, these alarm calls accelerated the adoption of more favourable site management (Vrabec et al. 2019), which possibly contributed to the high numbers during the 2016–2017 peak (Figure 1). They also propelled the establishment of the ex situ rearing in 2017 (from two larval nests: John 2020).

The low busts numbers emphasize the importance of metapopulation dynamics, both within the woodland (with individual openings viewed as inhabitable patches: Cizek and Konvicka 2005) and at a larger scale. Until recently, the bulks of annually produced larval nests concentrated at a few momentarily available clearings (Figure 2), although more even distribution may be achieved by active management actions. This is already under way, as forest managers added 7 ha of sparse canopy growths recently. Further 5 ha of this structure, plus 3 ha of active coppice, are planned for near future. Even with these measures, however, the appropriately managed area will remain much smaller than in the successfully managed *E. maturna* woodlands in Steigerwald, Germany (Dolek at el. 2018) and smaller than it was planned in Species Action Plan (AOPK ČR 2011).

The extremely low numbers in 2019 and 1920 testify that efforts to preserve strongly fluctuating insects within single sites are doomed in a long term (McLaughlin et al. 2002). Understanding this, the progeny of ex-situ populations was recently used to re-establish a population at a past site, 11 km distant Libice forest. In this 440.4 ha alluvial forest reserve, currently mostly in mature high forest state, a 1.5 ha clearing with abundant *Fraxinus excelsior* saplings was used to release 190 pre-pupation larvae in June and 3700 3rd instar larvae in July 2018; further 920 and 2320 4th instar larvae were released in June 2019 and 2020; respectively. Search for egg batches in 2019 yielded 24 of them, sixteen larval nests were recorded in 2020. Yet another transfer, planned for 2021, will target Žiželice forest (57.6 ha) situated 800 m apart (edge to edge distance) from Dománovice forest; a reserve was established there in 2017 and open canopy structure is being restored. If needed, the captive stock may also be used to support the donor Dománovice forest population.

A potential threat is represented by the ongoing ash dieback, caused by the fungus *Hymenoscyphus fraxineus* (cf. Skovsgaard et al. 2017). Decline of ashes is apparent at all the discussed Czech Republic sites. Planting of ash saplings, plus increasing the abundance of the alternative host *Lonicera nigra*, are considered as possible rescue measures.

If everything goes well, all the remnant deciduous woodlands in the Elbe river alluvium will be re-settled by *E. maturna* again, forming a regional metapopulation with individual woods, rather than clearings within the woods, functioning as local colonies. This assumes gradual adoption of forestry methods more favourable for the species (AOPK ČR 2011; Utínek 2014; Dolek et al. 2018). As the metapopulation theory predicts (Hanski 1999), such colonies should achieve mutually asynchronous abundance dynamics, stabilising the entire system against extinction via transfers of individuals (Heino and Hanski 2001). In Steigerwald, Germany, asynchronous local

dynamics plus migrations probably creates the irregularities in populations cycling (M. Dolek, personal communication). Similarly, eventual restoration of functional metapopulation in Czechia should stabilise the species` regional survival either via spontaneous migrations, or by occasional transfers carried out by the managers (cf. Porter and Ellis 2011; Kuussaari et al. 2015).

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